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# EVOLUTION OF THE TAPETUM

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**ABSTRACT**

*Purpose:* To review, contrast, and compare current known tapetal mechanisms and review the implications for the evolution of the tapetum.

*Methods:* Ocular specimens of representative fish in key piscine families, including Acipenseridae, Cyprinidae, Chacidae; the reptilian family Crocodylidae; the mammalian family Felidae; and the Lepidopteran family Sphingidae were reviewed and compared histologically. All known varieties of tapeta were examined and classified and compared to the known cladogram representing the evolution of each specific family.

*Results:* Types of tapeta include tapetum cellulosum, tapetum fibrosum, retinal tapetum, invertebrate pigmented tapetum, and invertebrate thin-film tapetum. All but the invertebrate pigmented tapetum were examined histologically. Review of the evolutionary cladogram and comparison with known tapeta suggest that the tapetum evolved in the Devonian period 345 to 395 million years ago. Tapeta developed independently in at least three separate orders in invertebrates and vertebrates, and yet all have surprisingly similar mechanisms of light reflection, including thin-film interference, diffusely reflecting tapeta, Mie scattering, Rayleigh scattering, and perhaps orthogonal retroreflection.

*Conclusion:* Tapeta are found in invertebrates and vertebrates and display different physical mechanisms of reflection. Each tapetum reflects the wavelengths most relevant to the species' ecological niche. With this work, we have hypothesized that the tapetum evolved independently in both invertebrates and vertebrates as early as the Devonian period and coincided with an explosion of life forms.

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## INTRODUCTION

The tapetum lucidum (shining carpet in Latin) is a catoptric device found in the eye of many vertebrates and invertebrates, which serves to increase the amount of light absorbed by the photoreceptors. The tapetum is proximal to the photoreceptors and may be located in either the choroid or deep retina in vertebrates and proximal to the retinular cells in invertebrates. The tapetum reflects the photons that were not initially absorbed after they passed through the photoreceptors. These reflector mechanisms provide the photoreceptors a second chance at absorbing the (reflected) light, thereby enhancing an organism's visual sensitivity. This device is often a layer, and it is especially useful in lower light conditions. Animals use a wide range of materials and techniques to provide tapetal reflectance, including guanine, riboflavin, triglycerides, pteridine, cholesterol, zinc, astaxanthin, and collagen.[1] Apparently, tapeta have evolved several times with these different mechanisms and represent convergent evolution of function.

From the Department of Ophthalmology, University of California, Davis, Medical Center (Dr Schwab); the University of California, Davis, School of Medicine (Dr Schwab, Mr Yuen, Dr Blankenship, Dr Fitzgerald); and the University of California, Davis, School of Veterinary Medicine (Dr Buyukmihci). Supported in part by an unrestricted grant from Research to Prevent Blindness, Inc, New York, New York, and by grant P30EY12576 from the National Institutes of Health.

## METHODS

Ocular specimens that are representative of fish in key piscine families, including Acipenseridae (*Acipenser medirostris*, the green sturgeon), Cyprinidae (*Cyprinus carpio*, the common carp), and Chacidae (*Ictalurus punctatus*, the channel catfish), were obtained from a local fish market. The ocular specimens were removed from the deceased fish. An ocular specimen of a member of the reptilian family Crocodylidae (*Alligator mississippiensis*, the American alligator) was obtained from Dennis Brooks, DVM, PhD, of the University of Florida in Gainesville. A fixed ocular specimen of the mammalian family Felidae (*Felis domesticus*, the domestic housecat) was obtained from Leslie Lyons, PhD, and David Maggs, BVS (hons), DACVO, of the University of California, Davis, School of Veterinary Medicine. A specimen of the Lepidopteran

family, Sphingidae (*Arctonotus lucidus*, the Pacific green sphinx moth), was obtained with the help of John Debenedictis, PhD, staff entomologist, Bohart Museum of Entomology, University of California, Davis, and the compound eyes were dissected from the specimen. Each of these ocular specimens was sectioned and stained with hematoxylin-eosin (HE), periodic acid–Schiff (PAS), or toluidine blue (TB), examined, and compared with one another histologically. The evolutionary relationship of the ocular specimens was examined and the cladistic position of each species established, evaluated, and compared.

## RESULTS

The eye of *A medirostris*, the green sturgeon, was found to contain a tapetum cellulosum. Although it resembles a tapetum fibrosum in some respects when stained (PAS), it has a cellular structure within the choroid immediately proximal to the pigment epithelium with from three to five cells aligned somewhat irregularly (Figure 1), especially when compared with the more regularly and definitely formed feline tapetum cellulosum. When stained with HE, the sturgeon eye revealed guanin granules in the superficial choroid (Figure 2). The retinal pigment epithelium (RPE) was generally clear, as is typical for animals with a choroidal RPE, but regularly spaced RPE cells contained a dense concentration of melanin with intervening clear RPE cells (Figures 1 and 2).

The tapetum lucidum of *C carpio*, the common carp, was reviewed and confirmed to be a retinal tapetum composed of guanin in an occlusible pattern. The light-adapted eye shows pigment drawn into the more inner portions of the retinal pigment epithelium and obscuring the guanin of the retinal tapetum (Figure 3).

The eye of *I punctatus*, the channel catfish, shows an occlusible retinal tapetum. A light-adapted retina shows pigment drawn up into the broad retinal pigment epithelial cells in a manner similar to the carp (Figure 4).

The eye of *Allig mississippiensis*, the American alligator, revealed fine opaque crystalline granules in the apex of the pigment epithelial cells, and represents a retinal tapetum. These granules were present in the dorsal half of the retina, although the stain (TB) has made the rodlike structures of the granules appear black (Figures 5A and 5B).

The eye of *F domesticus*, the domestic housecat, shows a regular tapetum cellulosum. This cellular structure consists of 6 to 12 flat and well-organized cells arranged in a regular distribution, resembling precision brickwork (Figure 6).

The compound eye of *Arct lucidus*, the pacific green sphinx moth, revealed a tapetum of modified tracheoles with chitin layers alternating with layers of air. The parallel layers of chitin and air have a long axis that is perpendicular to the long axis of the rhabdom. These chitinous layers are separated by a standard distance from rhabdom to rhabdom (Figure 7).

## DISCUSSION

### TYPES OF TAPETUM

Tapeta can be classified according to location in vertebrates and mechanism in invertebrates (Table I).

*Vertebrate Choroidal Tapeta*

Choroidal tapeta are the most common and are further classified as tapetum fibrosum and tapetum cellulosum.

Histologically, the simplest type is the tapetum fibrosum, which is found principally in mammals, including herbivorous ungulates (eg, elephants, horses, goats) (Figures 8 and 9), cetaceans (whales, dolphins), some marsupials (Tasmanian devil), and a rodent (*Cuniculus pacas*).[2,3] The tapetum fibrosum consists of extracellular collagen fibrils stacked in an orderly manner with the majority of the fibers running horizontally.[4] The number of layers of fibrils varies between species and can be up to several hundred thick.[2]

The most studied tapetum fibrosum among the ungulates is found in the cow. In this species, the tapetum is located posteriorly and dorsally. It is of variable thickness, increasing in thickness posteriorly. In species with a choroidal tapetum, the retinal epithelium in the area of the tapetum is unpigmented, allowing light to pass to be subsequently reflected by the tapetum. This contrasts with the pigmented retinal epithelium cells found in the same animal in nontapetal regions.[4]

The tapetum cellulosum is found in cartilaginous fishes (eg, sharks, dogfishes), sturgeons (Figure 1), lobe-finned fishes (coelacanths and lungfishes), seals, prosimians (eg, bush babies [Figure 10], lemurs), and most mammalian carnivores (eg, cats, dogs [Figures 6 and 11]).[1,5-7] This tapetum is composed of regular cells in layers of variable thickness, containing a variety of reflective material.[3,8,9]

In the coelacanth (*Latimeria chalumnae*), the tapetum cellulosum consists of hexagonal constant-thickness stacks of guanine crystals within the individual cells. This tapetum emits a greenish-yellow luminescence in the live specimen, with a broad maximum wavelength of reflection peaking at 476 nm, which corresponds to the peak of the wavelength of light that penetrates to depths of 7,500 feet, where the animal is found. This choroidal tapetum underlies the entire retina and appears bright silvery upon dissection. Elasmobranchs also have tapeta composed of guanine, but their tapeta differ from those of the coelacanth and others in that they are occlusible. The tapetal cells alternate with, and are separated from, one another by melanocytes that extend beyond the tapetal cells to

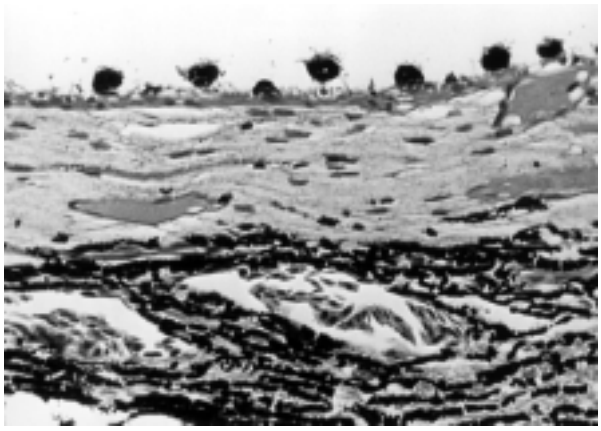

**FIGURE 1**
Sturgeon choroid stained with periodic acid-Schiff (x20). Retinal pigment epithelium (RPE) can be seen at top of photograph. Note periodicity of pigment in RPE. Intervening RPE cells contain no pigment.

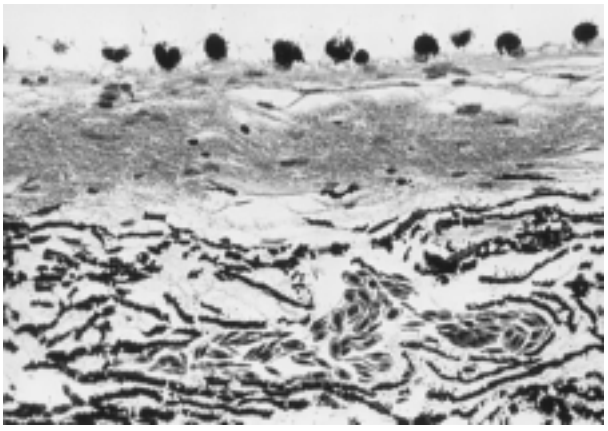

**FIGURE 2**
Sturgeon choroid stained with hematoxylin-eosin (x20). Note guanine crystals in superficial choroid immediately beneath retinal pigment epithelium (RPE). These crystals are seen as a grey coloration below pigmented deposits of RPE. Note periodicity of pigment in RPE.

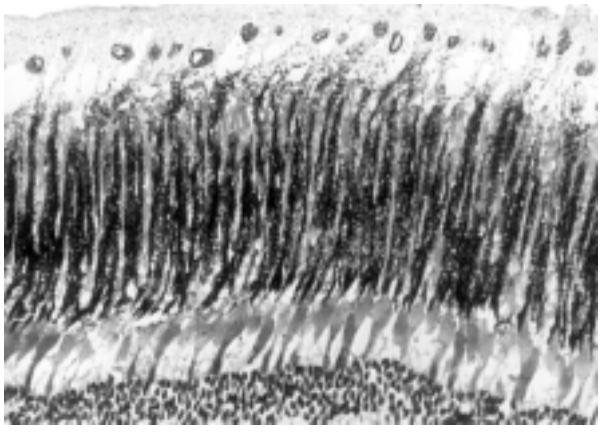

**FIGURE 3**
Carp retina stained with hematoxylin-eosin (x20). Note broadly distributed melanin throughout most of retina. This light-adapted retina exhibits an occlusible retinal tapetum. Cell bodies with nucleus of retinal pigment epithelium (RPE) can be seen at bottom of photograph. Note how little pigment is seen near base of RPE cell.

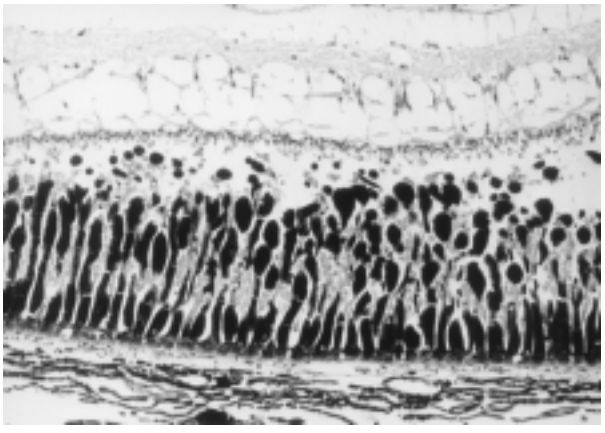

**FIGURE 4**
Light-adapted catfish retina stained with hematoxylin-eosin (x10). Note occlusible tapetum with the melanin pigment drawn nearly to outer nuclear layer, obscuring both tapetum and rod outer segments.

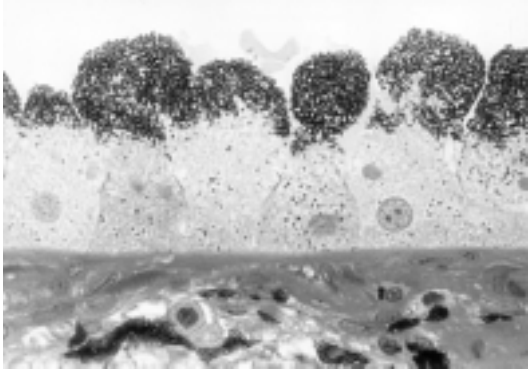

**FIGURE 5A**
Light-adapted American alligator retinal pigment epithelium (RPE) in a nontapetal region with pigment granules visible at tips of RPE stained with toluidine blue (x40). This retina is only partially occlusible and has probably lost the ability to be truly occlusible but does show some pigment migration in light adaptation. Pigment in the RPE is present in nontapetal regions of the eye.

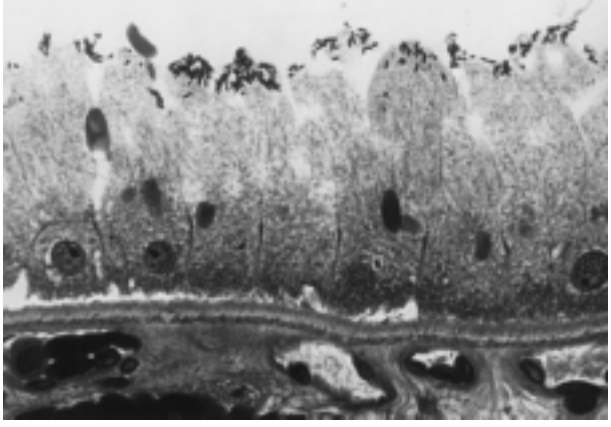

**FIGURE 5B**
Light-adapted American alligator retinal pigment epithelium (RPE) in tapetal region stained with toluidine blue (x40). Note black, flat platelike crystals in tips of RPE cells in contrast to granules of pigment seen in 5A. Many crystals were lost in preparation of specimen.

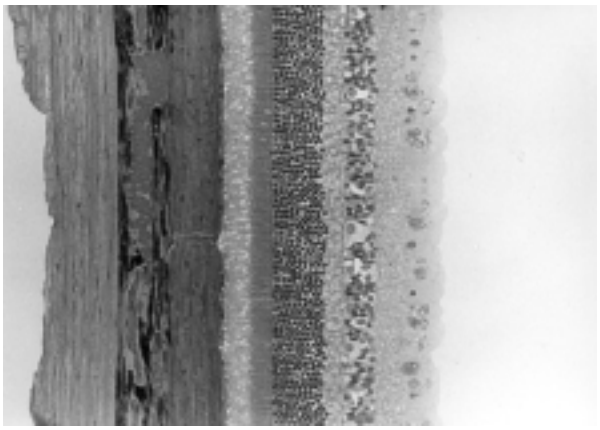

**FIGURE 6**
Cat choroid stained with toluidine blue (x20). Note regular tilelike cellular structure beneath retinal pigment epithelium (RPE) and photoreceptor outer segments. These cells in tapetum cellulosum are filled with many smaller platelike structures or rodlets seen with ultrastructural investigation.

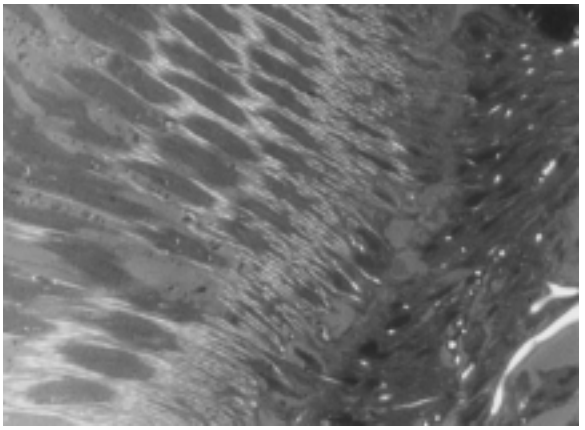

**FIGURE 7**
Compound eye of Pacific green sphinx moth stained with toluidine blue (x40). Larger tracheoles can be seen to right of photograph as clear spaces. As tracheoles become smaller (going toward left on photograph), they can be seen as small, clear circles. Tracheoles that become tapetum can be seen in about the middle of photograph as fine striations. Larger blue ovals toward left of photograph are undulations of rhabdoms of individual ommatidia.

intervene between the tapetal cells and incoming light. The melanocytes migrate in conditions of increased light to occlude the elasmobranch tapetum.[5]

The RPE and the choroidal tapetum of the sturgeon show another interesting feature. The regular deposits of pigment may serve a heretofore unrecognized purpose. The regular spacing of pigment would create a grating though which light could be channeled upon reflection, preventing extraneous photons from being scattered to adjacent photoreceptors. This would assist in the elimination of the glare of the reflection from the tapeta, which would otherwise lead to the degradation of the image owing to the scatter of the extraneous rays, and would be an alternative to an occlusible tapetum as seen in the elasmobranchs.

*Vertebrate Retinal Tapeta*

The retinal tapetum has been found in some lampreys, certain bony fishes, crocodiles, goatsuckers, the Virginia opossum (*Didelphys virginiana*) (Figure 12), gar fishes, some old-world fruit bats, and many teleosts (Figures 3 and 4).[1] The retinal tapeta of fish have been further categorized as those that contain small particles in spheres or cubes, which are classified as diffuse reflectors, and those containing layered crystals, classified as specular reflectors. Specular reflectors function much like a mirror, whereas diffuse reflectors are more like the reflections from a rough surface and may use Mie scattering as their mechanism.[1,9] Diffuse tapeta can be found in many teleosts, including certain carp and cusk eels. Specular tapeta can be found in some lantern fish and other abyssal fish.[9]

Some species of lamprey have both diffuse and specular mechanisms. The reflecting material in teleost spheres includes nonpigmented materials (such as guanine, uric acid, and purines) and pigmented materials (including pteridine, lipid, astaxanthin, and melanoid compounds).[1] This represents a subclassification of the small-particle or diffuse reflectors.

In reptiles, only the crocodile and alligator have a tapetum, and it is found in the retinal pigment epithelium. This tapetum consists of several layers of crystalline platelets of guanine arranged in parallel. The tapetum appears to be somewhat occlusible in certain species, such as the American alligator, and this could be explained by the diurnal and nocturnal potential of that species.[10] This contrasts with another crocodile, the *Caiman sclerops*, a nocturnal animal, which does not have an occlusible tapetum. The tapetum of the *C sclerops* also consists of guanine crystals diffusely scattered within the RPE.[11]

The retinal tapetum of the opossum (*D virginiana*) is a semicircular area in the dorsal fundus. The reflecting material consists of lipoidal spheres scattered throughout the epithelial cells.[12] The tapeta of the crocodile and the opossum function as diffuse reflectors.

Amphibians, apparently, do not have tapeta, although a bright reflex is found in many of these species. The source of this bright reflection is unknown at present but does not conform to the currently understood mechanisms of any tapeta.

**INVERTEBRATE TAPETA**

*Pigmented Tapeta*

The invertebrate tapeta can be categorized as light-scattering pigments and those using thin-film interference.

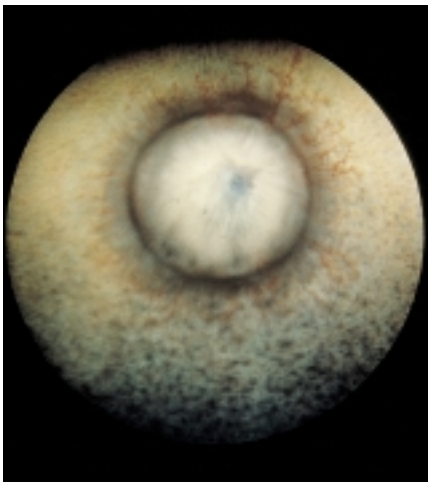

**FIGURE 8**
Funduscopic photograph of left eye of 6-year-old female African elephant. The elephant has a tapetum fibrosum.

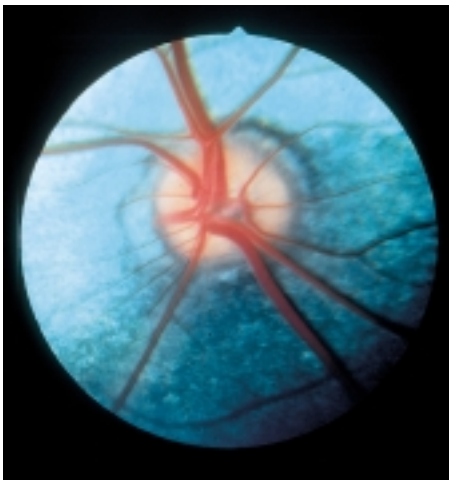

**FIGURE 9**
Funduscopic photograph of right eye of 6-month-old castrated male mixed-breed goat. The goat has a tapetum fibrosum.

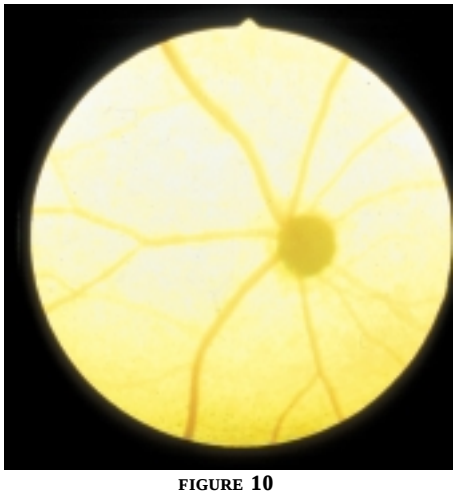

**FIGURE 10**
Funduscopic photograph of a galago. Bush babies have a tapetum cellulosum.

**FIGURE 11**
Funduscopic photograph of left eye of an adult female mixed-breed of dog. Dogs have a tapetum cellulosum.

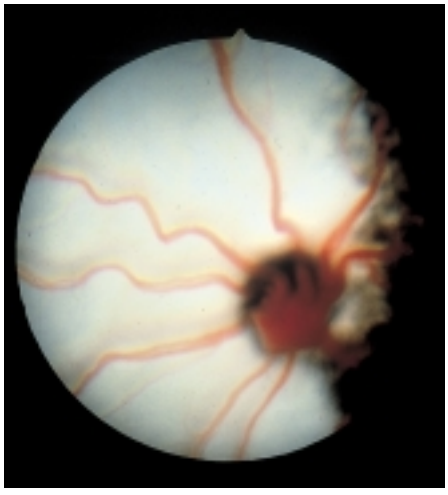

**FIGURE 12**
Funduscopic photograph of right eye of adult male American opossum with retinal tapetum.

**TABLE I: TAPETA IN THE ANIMAL KINGDOM**

| ANIMAL KINGDOM | | | | | | NO TAPETUM | CHOROIDAL TAPETA | | RETINAL TAPETA | LIGHT-SCATTERING TAPETA | THIN-FILM TAPETA | TAPETA REFLECTING MATERIAL | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | FIBROSUM | CELLULOSUM | | | | UNPIGMENTED | PIGMENTED |
| Fishes | Jawless Fishes | Lampreys | | | | ✓ | | | | | | | |
| | | Hag Fishes | | | | ✓ | | | | | | | |
| | Jaw Fishes | Sharks/Dog Fishes | | | | | | + | | | | Guanine | |
| | | Sturgeons | | | | | | + | | | | Guanine | |
| | | Garpikes | | | | | | | + | | | | Asthaxathine |
| | | Bony Fishes | | | | | ? | + | + | | | Several Materials | Several Materials |
| | | Coelacanths | | | | | | + | | | | Guanine | |
| | | Lung Fishes | | | | | | + | | | | Not Reported | Not Reported |
| Amphibians | | Salamanders | | | | ✓ | | | | | | | |
| | | Frogs & Toads | | | | ✓ | | | | | | | |
| Reptiles | | Crocodiles and Alligators | | | | | | | + | | | Guanine | |
| | | Most reptiles | | | | ✓ | | | | | | | |
| Birds | | Goatsuckers (Nightjars) | | | | | | | + | | | | Lipid |
| | | Most Birds | | | | ✓ | | | | | | | |
| Mammals | | Monotremes | | | | ✓ | | | | | | | |
| | | Marsupials | Opossums | | | | | | + | | | Lipid (Birefringent) | |
| | | | Tasmanian Wolves | | | | + | | | | | Collagen | |
| | | Placentals | Whales & dolphins | | | | + | | | | | Collagen | |
| | | | Elephants & Most Hooved Animals | | | | + | | | | | Collagen | |
| | | | Carnivores (Cats & Dogs) | | | | | + | | | | | Zinc protein |
| | | | Horses | | | | + | | | | | Collagen | |
| | | | Primates | Lower (Bush Babies & Lemurs) | | | | + | | | | | Riboflavin |
| | | | | Higher | Aotus Monkeys | ✓ | | | | | | | |
| | | | | | All Other Higher Primates | ✓ | | | | | | | |
| | | | Rodents | Cuniculus Pacas | | | + | | | | | Collagen | |
| | | | | Most Rodents | | ✓ | | | | | | | |
| | | | Seals | | | | | + | | | | | Believed to be Zinc |
| | | | Fruit Bats | | | | | | + | | | Phospholipid (birefringent) | |
| Mollusks | | Scallops | | | | | | | | + | | Guanine | |
| Arthropods | | Crustaceans | Lobsters & Shrimp | | | | | | | | + | | Lipid |
| | | Arachnids | Scorpions | | | ✓ | | | | | | | |
| | | | Spiders | | | | | | | + | | Guanine | |
| | | Insects | Dragonflies | | | | | | | | + | Chitin | |

In the eyes of crustaceans, light is reflected back to the rhabdoms by white or lightly colored pigments, including purines or pteridines. The reflection is less useful over shorter wavelengths but is effective over much of the spectrum and can almost double light capture.[9,13]

The tapeta of mesopelagic shrimps vary greatly between species, depending on the depth at which they live, and probably corresponding to individual ecological niches and the specific wavelengths required. Histologic examination of the tapetum shows that it is incomplete dorsally in some species from the upper mesopelagic zone (*Sytellaspic debilis*, *Oplophorus spinosus*), with the amount of reflecting material increasing ventrally. Not surprisingly, peak transmission of light in oceanic species is in the blue-green region of the spectrum (450 to 500 nm). Visual pigments in crustaceans show absorbence between 470 and 490 nm, and reflecting materials appear white. The tapetum is located between the rhabdom and basement membrane.[14] The tapetum is complete in some deep-water species (*Systellaspis crsitata*, *Acanthephyra kingsleyi*, *Acanthomysis pelagica*) and is believed to be beneficial because of the lower levels of ambient light at greater depths. *Acanthephyra purpurea* has a thick tapetum peripherally but no tapetum in the central part of the eye. This is thought to interfere with the ability of predators to detect this shrimp because of decreased eye shine centrally. The tapetal adaptations of these species are believed to increase sensitivity to the dim upwelling irradiance and to bioluminescence.[14]

*Thin-Film Invertebrate Tapeta*

Thin-film interference is used by some invertebrates to construct a reflective tapetum. The best examples of this mechanism are found in the lycosid spiders, scallop (*Pecten maximum*), ostracod crustaceans, cockle (*Cardium edule*), and rotifers.[13,15-18] In the ctenid spider, a type of lycosid, the tapetum is located proximal to the rhabdomeres in the secondary eyes, while the primary anteromedial eyes do not have a tapetum. The secondary eyes are built around a "gridiron" tapetum, consisting of parallel strips of reflecting material forming a double ladder–like array.[15] The reflecting material in lycosid spiders has been reported as guanine.

Tapeta have also been described in only a few mollusks. In the scallop (*P maximum*), for example, square guanine crystals have been described as a tapetum.[16]

Nocturnal moths and diurnal butterflies both possess a tapetum constructed of modified tracheoles, or airway cells.[17] The tapeta in nocturnal moths consist of air layers next to chitin, providing a large difference in refractive indices, which provides for a higher percentage of reflected light. The tapetum of these nocturnal moths appears blue-green, whereas in diurnal butterflies each rhabdom possesses its own tapetum. In many diurnal butterflies, the tapetum consists of up to 40 overlying layers, which are regularly spaced cuticular plates, each separated from its neighbors by air spaces. Because the tapetum varies in thickness, and relies on constructive interference, dorsally it tends to reflect blue light, whereas ventrally it tends to reflect red.[13,18,19]

**MECHANISMS OF THE TAPETUM**

Although much is known about the structure and biochemical composition of the tapetum, there is considerably less information on the spectral reflectance characteristics and mechanisms.[1,13] Thin-film constructive and destructive interference probably plays a prominent role in the reflective mechanisms of the tapeta of many of these animals. Layers of crystals, or other structures with differing indices of refraction at a thickness of $\lambda/4$ of the maximal wavelength of reflected light, support the theory that constructive interference is involved. Theoretically, 15 to 20 layers at $\lambda/4$ should provide nearly 100% reflection of light at a wavelength of $\lambda$.[17]

Diffusely reflecting tapeta have been described in which reflection off a rough surface occurs and enhances the sensitivity of the retina, but this cannot be constructive interference. Mie scattering has been proposed as a mechanism for diffusely scattering tapeta, but this has not been studied in detail.[20,21] Rayleigh scattering (scattering by particles smaller than the wavelength of light with preferential scattering of the shorter wavelengths, similar to the phenomena of our atmosphere creating a blue sky), may also be involved, especially for the tapetum fibrosum.[20,22]

Some butterflies employ a unique form of orthogonal retroreflection that juxtaposes yellow next to blue regions, synthesizing a green color in their wings. A concave surface composed of flat and inclined regions appears yellow and blue, respectively. The juxtaposition of these colors appears green because these regions produce individual streams of photons too small to be resolved individually.[23,24]

Orthogonal retroreflection has never been studied as a potential mechanism for tapetal reflection, but could be involved, especially in invertebrate thin-film tapeta.[1] In the vertebrate world, the duplex retina of *Lestidiops*, a mesopelagic deep-sea teleost, has an anatomical configuration consistent with this form of reflection.[25] Other animals that may have employed orthogonal retroreflection include the bigeye fish (*Hybopsis amblops*) and cat (*F domesticus*). The tapetum of bigeye fish is actually a mosaic of different-colored spots, where measurements of minute, singly colored areas give spectral curves with restricted bands and expected side oscillations. The spectrum of the cat tapeta is variable between animals from green to yellow, and the color varies within the eye. The cat's tapetum is composed of bundles of rodlets, when viewed microscopically, and there appear to be different colors at varying depths.[1]

**PIGMENTED COLORS FORMING A TAPETUM**

The mechanism of individual colors produced by the tapetum has not been well studied. Constructive interference provides structural color, involving layers having the thickness of 1/4λ (where λ is the wavelength of light to be reflected), and has been proposed as a common mechanism. Some tapeta, however, contain pigmented reflecting crystals. In such animals, the appearance of these tapeta correlates with the pigmented color of these reflecting crystals. For example, the galago tapetum is composed of isoalloxazine or riboflavin crystals possessing a yellow hue.[26] The tapetum of the garpike has also been reported as being made up of yellow pigments.[27] A red pigmented tapetum can be found in characin fish and garfish.[28,29] The pigment is found enclosed in spheres in the retinal pigment epithelium. The reflecting material of characin fish, catfish tapetal pigment, consists of oligomers of 5,6-dihydroxindole-2-carboxylic acid combined with decarbox-ylated S-adenosylmethionine.[30] The pigmented tapetum has conferred an advantage to deep-sea fish that exist in an environment where the predominant wavelength of light is 475 nm. Most animals at these depths have photo-receptors that predominantly absorb light at this wavelength, since that is the only wavelength that penetrates to those depths.

A mesopelagic species of fish, *Malacosteus niger*, has evolved with a mechanism that allows it to take advantage of this downwelling blue light as well as possessing red light-emitting organs (photophores) located ventrally and sub-orbitally. These red photophores emit red light that is not recognized by the photoreceptors of most deep-sea animals. The photophores are larger than most photophores, suggesting that they may assist the *M niger* in illuminating prey or signaling other individuals of the same species. It is believed that *M niger*, and not other deep-sea animals, is able to absorb the red light emitted by its own photophores because it possesses a pigmented, diffused, scarlet-red tapetum that reflects the red light emitted by the photophores. This may allow the *M niger* to effectively visualize prey undetected, as well as communicate with others of their species, without alerting their predators.[28,30,31]

**EVOLUTION OF THE TAPETUM**

The timing of the evolution of the tapetum will probably never be determined exactly; however, we provide a model for the possible development of the tapetum according to existing evidence (Figures 13 and 14). Vertebrates are believed to have evolved from the pikaia, a primitive invertebrate and ancestor to the modern-day amphioxus. The pikaia existed in the Precambrian era, approximately 570 million years ago.[32] In the Silurian period (410 to 430 million years ago), fossils of the ostracoderm, the ancestor to the modern-day agnatha, had been discovered. Tapeta do not occur in amphioxus or agnatha; therefore we make an assumption that tapeta did not exist in ostracoderms. Though fossil history does not exist, Placoderms, Chondrostei, and lobe-finned fish are all assumed to have the ostracoderm as a common ancestor, on the basis of physical characteristics.

In the Devonian period (345 to 395 million years ago), all three orders may have developed tapeta independent of each other, based on their modem progeny, namely, sharks (Placoderm), sturgeons (Chondrostei), and coelacanths (lobe-finned fish). These three orders of fish all possess a tapetum cellulosum, suggesting that this tapetum may have been the first type of tapetum to evolve in vertebrates. These species have similar enough tapeta that they may have had a common ancestor with a tapetum developing at approximately the Devonian period or, at the earliest, the very late Silurian. It is unlikely that the tapetum appeared earlier, because hagfish and most lampreys do not have tapeta and it is believed these species separated in the Silurian period. The development of the tapetum independently in fish might have occurred to allow them to explore deeper depths of the ocean, where light was not as prevalent. Conquering the depths of the ocean may have provided sources of food not previously accessible, such as detritus.

The lobe-finned fish ancestor, closely related to the coelacanth and lungfish, is believed to be the predecessor to amphibians on the basis of physical characteristics.[32-34] While amphibians may have possessed a tapetum at one time, none has been reported in modern species.[35] It would appear that, through evolution, either amphibians lost the ability to produce a tapetum or their lobe-finned fish ancestors did not possess one. Amphibians are commonly accepted as the ancestors of reptiles. The *Eryops* genus is believed to have been primitive reptiles that evolved from amphibians, dating back to the Permian period (220 to 280 million years ago). The crocodile, believed to have descended from these primitive reptiles, evolved retinal tapetum composed of guanine. This suggests that crocodiles independently evolved or re-evolved a similar retinal tapetum employing guanine, well described in jawed fishes. Guanine as a reflecting material is found widely in animals with tapeta. The crocodile also uses guanine as its reflecting material, as do many fish, the wolf spider, and many other unrelated species. The crocodile tapetum is located dorsally and temporally. It has been hypothesized that the location of the tapetum in the crocodile correlates with the need to improve the animal's ability to see in murky waters below it.[20]

Mammals evolved from mammallike reptiles, which presumably did not have tapeta. This is supported by monotremes, which evolved independently from other mammals and belong to the order Docodonta. They have eyes that are much more like reptilian eyes than mam-

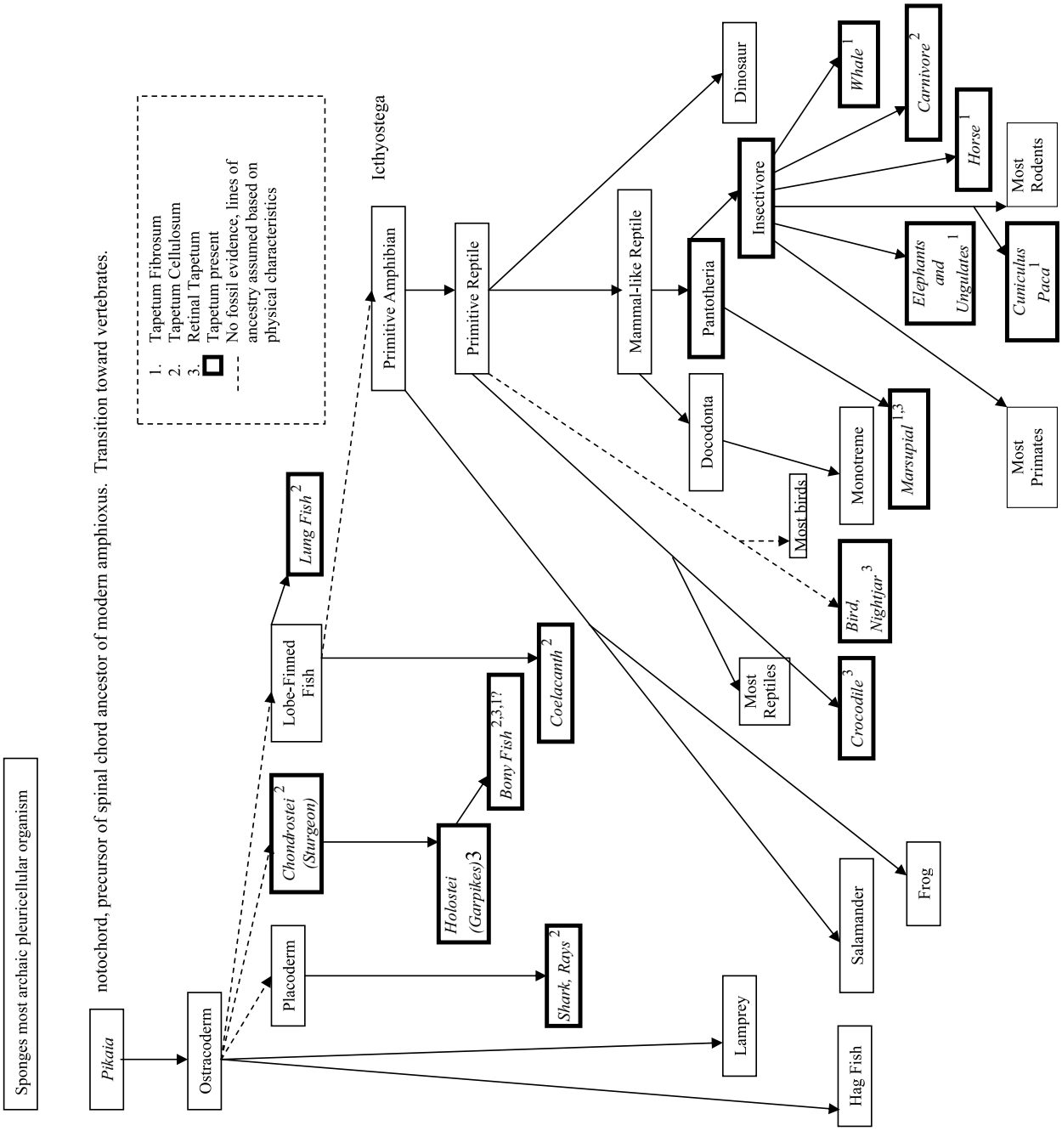


**FIGURE 13**
Evolutionary diagram of vertebrate tapeta.

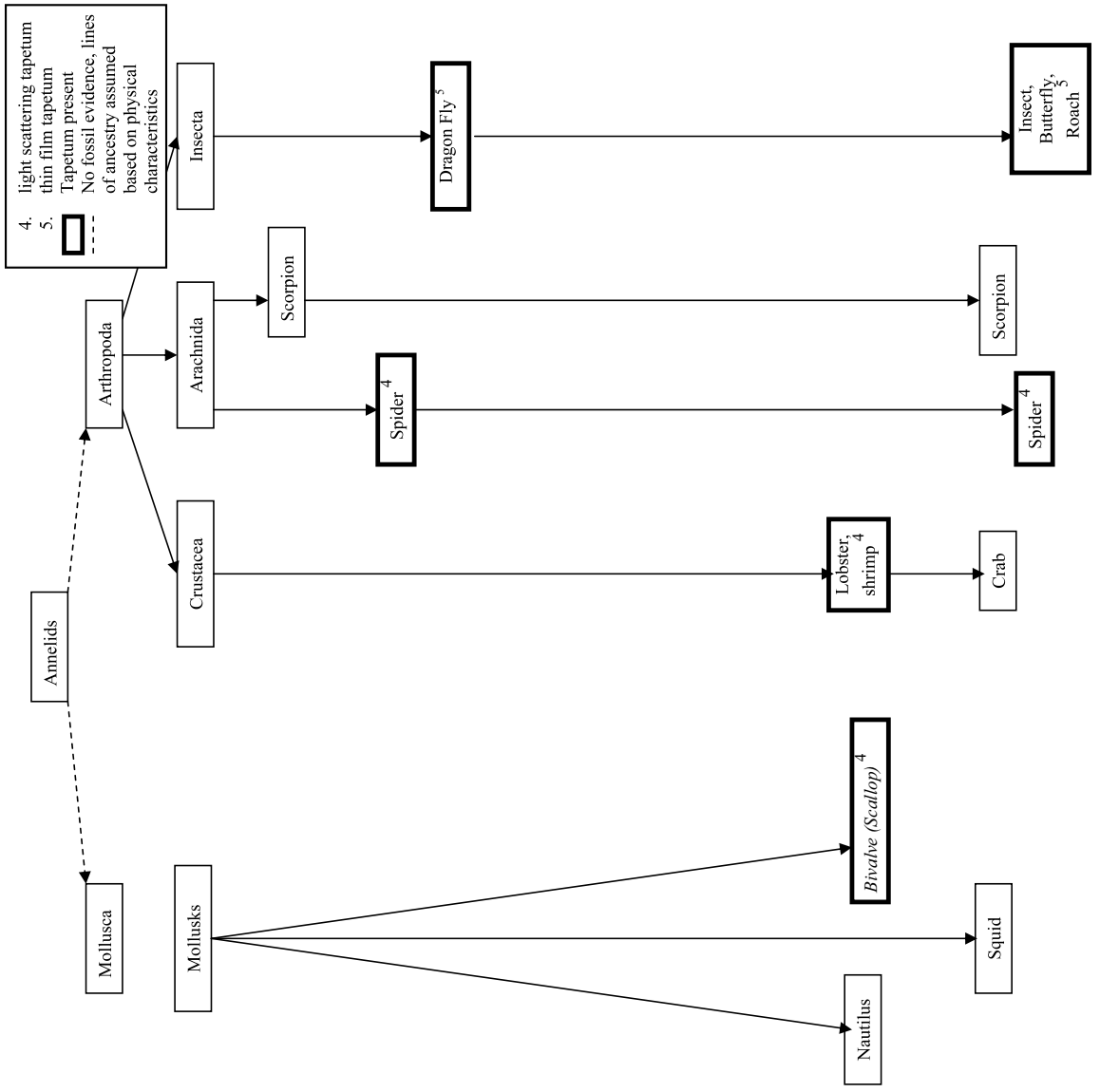


**FIGURE 14**
Evolutionary diagram of invertebrate tapeta.

malian eyes, and they do not have tapeta.[13] With the exception of monotremes, all other mammals belong to the order Pantotheria, which gave rise to marsupials and insectivores, from which all other mammals were probably derived. There are numerous examples of marsupial tapeta, but there are some interesting differences. The Virginia opossum has a retinal tapetum with lipoid reflecting material, while the Tasmanian devil has a tapetum fibrosum, suggesting independent evolution, and no common ancestor with a tapetum. Many other, but not all, mammals have tapeta, including ungulates, cetaceans, carnivores, rodents, and prosimians.[1,13,18,35] It seems that the tapetum was probably not present in the mammal-like reptile, but appeared later in mammals in the Cenozoic era, no more than 60 million years ago, when the the tapetum seems to have evolved independently once again. Mammalian tapeta include tapetum fibrosum, cellulosum, and retinal tapeta, similar to yet different from previously evolved tapeta. Somewhat unexpectedly, tapeta are also found in strictly diurnal mammals, such as the Indian mongoose, ungulates, and dogs,[1,36] although dogs and ungulates may be functionally nocturnal.

The tapetum has been reported in only two phyla of invertebrates, Mollusca and Arthropoda (Figure 14). On the basis of physical characteristics, both phyla are assumed to have evolved from Annelids in the Precambrian era (1,000 million to 570 million years ago). The common ancestor to mollusks and arthropods–annelids–do not have, and probably never did have, a tapetum. Among only a few mollusks, a guanine tapeta appears to have evolved independently of the tapeta of arthropods with different mechanisms. Among the mollusks, cephalopods possess some of the most advanced eyes among the invertebrates, and even have "camera-style" eyes like most vertebrates, but they do not possess tapeta.[36]

Tapeta have been reported in three classes of arthropods: Arachnida. Insecta, and Crustacea. These classes appear to have evolved as separate lineages during the Precambrian era. The tapetum in invertebrates may also have evolved in the Devonian period. Spiders are credited as one of the first predators on land and can be traced back 395 million years ago, according to the fossil record.[32,33] This was prior to the evolution of flying insects that spiders commonly entrap in their webs.[32] Hence, prehistoric spiders probably hunted their prey much like lycosid spiders of today. Although the invertebrates and vertebrates both probably developed tapeta in the Devonian period, the solutions were very different for similar results. As opposed to fish, which probably developed tapeta to explore the depths of the ocean, spiders probably developed tapeta to allow them to take advantage of nocturnal conditions or to protect themselves against predators. Like sharks, the lycosid spider employs guanine as its reflecting material organized into a thin-film reflector. In the class Insecta, dragonfly fossils have been dated to 350 million years ago, in the late Devonian to early Carboniferous period, and probably represent the earliest insect tapeta. Tapeta have been reported in dragonfly ocelli.[6] Because their common ancestor did not have tapeta, it appears that the dragonfly and the arachnids evolved tapeta independently of each other. Crustaceans, such as the lobster and shrimp, have pigmentary tapeta, appear to have evolved independently of insects and arthropods, and have different mechanisms.[23,24]

## CONCLUSIONS

Tapeta are found in both vertebrates and invertebrates. Not surprisingly, it appears that tapeta have a tendency to reflect wavelengths most relevant to the animal. The tapeta in vertebrates are located in either the choroid or deep retina. Choroidal tapeta are further classified as tapetum cellulosum and tapetum fibrosum, according to their appearance. The tapetum cellulosum is composed of reflecting cells stacked in depth, like tile work. The cells contain numerous refractile bodies with an orderly arrangement. The tapetum fibrosum is acellular and composed of stacks of densely packed collagen fibrils. Retinal tapeta are found in the form of small granules in spheres and cubes or regularly arranged stacked thin platelets. These tapeta reflect light by diffuse reflection and specular reflection, respectively.

A variety of reflecting material has been reported in invertebrates and vertebrates, including nonpigmented material such as uric acid, guanine, chitin, and collagen, and pigmented material such as cholesterol esters, lipids, pteridine, and astaxanthin.[1] Nonpigmented reflecting crystals appear to produce colors structurally, while the color produced by pigmented reflecting crystals may be a result of their pigmentation.

Mechanisms by which tapeta reflect light are incompletely understood. Constructive interference appears to be a common mechanism by which some tapeta reflect light; it does not appear, however, to be the only mechanism involved in all tapeta. In addition to thin-film interference, diffuse reflection and pigmented color granules are probably involved in tapetal reflection. Orthogonal retroreflection, a newly discovered mechanism of reflection in butterfly wings, has never been studied as a potential mechanism in butterfly tapeta and may be a more common mechanism than currently recognized.

We hypothesize that the tapetum may have arisen independently in both invertebrates and vertebrates as early as the Devonian period (390 to 345 million years ago). In vertebrates, the guanine choroidal tapetum may have arisen in sharks, sturgeon, and lobe-finned fish inde-

pendent of each other, or if there were a common ancestor, it originated in the Devonian era. This coincides with an explosion in the evolution of many different types of marine life. It appears that the choroidal tapetum was the first type of tapetum to evolve in vertebrates, with retinal tapeta appearing independently in other tetrapods.

The invertebrate tapetum appears to have evolved first in spiders, in the Devonian period, and consists of a diffusely reflecting guanine tapetum. All of these tapeta employ unpigmented guanine as their reflecting crystals, and guanine was probably the first reflecting material employed. The evolution of the tapetum appears to be highly convergent, but often with subtle differences in development. Tapeta probably arose separately in invertebrates and vertebrates and even within these broad groups, the tapetal mechanisms appear to have distinctly and separately evolved, yet with surprisingly similar mechanisms.

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## DISCUSSION

DR RALPH C. EAGLE, JR. Tapeta are mirrorlike structures in the choroid or outer retina that have evolved to subserve vision in low levels of light. Essentially, they reflect photons back from the eyewall, thereby increasing the probability of capture by the photoreceptors. Tapeta characteristically are found in nocturnal animals like the raccoon and fish or marine mammals like the whales that frequent the ocean depths. The authors' studies and literature review indicate that tapeta have evolved convergently in both vertebrates and invertebrates and have a tendency to reflect the wavelengths that are most relevant to the animals' environment. They hypothesize that they may have arisen as early as the Devonian period.

People probably are most familiar with the tapetal reflex or eye shine of cats. Electron microscopy of the feline tapetum cellulosum discloses myriad rodlets of osmiophilic material thought to be a zinc cysteine or taurine compound in the cytoplasm of its cells, which are stacked like brickwork. The rodlets are arranged in an exquisitely regular fashion that is reminiscent of the spacing of collagen fibrils in the corneal stroma, but the diameter of the tapetal rodlets is greater than that of corneal collagen (120 nm versus 22 to 35 nm) and they are spaced further apart (2 to 300 nm versus 42 nm).[1] Presumably, the size and spacing of the rodlets and fibrils are consistent with constructive interference and reflection in the feline tapetum and with destructive interference and transparency in the cornea.

Although tapeta occur in nocturnal prosimians like the bushbaby, they normally are not found in healthy higher primates, including man. Abnormal fundus reflexes that have been likened to tapeta do occur in several ocular diseases, however. Leber applied the term *tapetoretinal dystrophy* to a variety of heredodegenerative retinal diseases including retinitis pigmentosa and fundus flavimaculatus. According to Duke-Elder, this term is derived from the tapetum nigrum or black carpet, an archaic term for the retinal pigment epithelium.[2] Leber thought that primary defects in the RPE were responsible for such disorders.

Shiny reflective fundus reflexes reminiscent of tapeta do occur in patients who have some of these heritable disorders, including Oguchi's disease,[3,4] X-linked cone dystrophy,[5] and the female carrier state of X-linked retinitis pigmentosa.[6,7] Oguchi's disease is a form of stationary night blindness caused by mutation in the gene for arrestin, a molecule involved in the recovery phase of light transduction. Ophthalmoscopy discloses a shiny golden fundus reflex in light-adapted patients with Oguchi's disease. This golden reflex disappears after the patient has been kept in the dark for several hours, and this is called the Mizuo-Nakamura phenomenon. The eye shine in Oguchi's disease might be considered a paradoxical tapetum, for it is present in the light and disappears in darkness. I am unaware if patients with Oguchi's disease have been observed to have abnormal eye shine under nonclinical conditions.

A classic example of a human tapetal reflex occurs in children who have retinoblastoma. In 1767, Hayes initially noted that the pupil in retinoblastoma had "a bright look, something resembling a cat's eye in the dark."[8] The "amaurotic cat's eye reflex" is an older alternative term for leukocoria.

On a lighter note, red, glowing eyes purportedly occur in a variety of creatures that are legendary or of questionable authenticity. The latter include the Jersey Devil, the Chupacabra or goatsucker of Puerto Rico, the Mothman of Point Pleasant, West Virginia, and the Sasquatch or Bigfoot of the Pacific Northwest and its Florida relative the Myakka "skunk ape."[8] Because higher primates lack tapeta, the presence of a tapetal reflex in Bigfoot, would seem to cast doubt on the authenticity of this humanoid unless one postulates yet another example of convergent evolution. A photograph said to depict the Myakka skunk ape is posted on a cryptozoological Web site on the Internet.[9] The hairy creature in the photo does have glowing eyes.

Various sources on the Internet also indicate that creatures from the infernal regions have red glowing eyes. In fact, red eye shine, often transitory in nature, has become a ubiquitous cinematic convention for portraying devils, demons, and demonic possession in the movies. One might speculate that the latter association might stem from the eye shine of cats, which were thought to be agents of the devil in medieval Europe. Images in our collective racial memory of large feline predators lurking in the shadows around our ancestors' campfires might be a contributing factor.

The association of red eye shine with Satan and demonic possession probably is a major factor behind the general population's revulsion with the common artifact of flash photography called "red eye". Our repugnance with this unnatural appearance has led to the development of cameras equipped with repetitive flashes designed to reduce or eliminate this photographic artifact by inducing pupillary miosis before photos are taken. Computer image processing software programs such as Adobe Photoshop are also touted for their ability to correct red-eye digitally.

Red-eye reduction in amateur photography theoretically could have adverse medical consequences by delay-

ing the diagnosis of retinoblastoma. Not infrequently, parents of affected children initially detect leukocoria as a difference in character of the "red eye" in their child's photos. Photographic pseudoleukoria may occur in healthy children, however, if the flash fortuitously happens to illuminate the optic disk in an appropriately adducted eye. I am aware of such an incident of photographic pseudoleukocoria that involved an ocular oncologist's child, prompting expedient ophthalmoscopy.

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DR ALFREDO A. SADUN. I am fascinated by the strategies that the tapetum use. If the tapetum were to be a quarter wavelength in thickness, like a lens coating, then a quarter in, quarter out means that the light's going to be half a wavelength out of phase and you have destructive interference. But that's only for that given wavelength; for every place you have destructive interference, 25% longer or 25% shorter wavelengths will have constructive interference. So the trade-off is always choosing what you are going to construct and what you are going to destruct. So my question for Dr Schwab is, Were the shifts along the strategies of various species such that one animal like the cat is doing constructive interference at yellow and destructive interference at blue and probably destructive at the infrared? Were there shifts that reflected the animal's behavior and needs?

DR TERRY J. ERNEST. Where do these extraordinarily difficult crystal structures in biology work, what cells make them, where do they come from? What's evolution doing to these crystals? The last thing you want to do is put a mirror inside the eye. If you want to get better vision, you go to the standard, the eagle, and you add a fovea, but you don't put a mirror in there, which would cause terrible reflections everywhere regardless of thickness.

DR IVAN R. SCHWAB. It is difficult to know the process that selects tapeta as we realize that evolution isn't a force as you think of a choice; evolution is a random process—it works by mistakes and time. So, in answer to the question, I don't know the answer, but my guess would be to maximize photons in darkness for prey capture. What are the strategies and why the different colors? That is certainly unclear, especially since certain species, such as cats, may have different colors or no color at all, depending on the species, depending on the breed; in other words, colors can be bred out. So in answer to that first question, the strategy isn't clear because it's even different from one cat to another. But, as I say, the strategy almost certainly is for activity in darkness.